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THE FIRST SKELETAL RECORD OF THE CRETACEOUS ENIGMATIC SAWFISH
GENUS PTYCHOTRYGON (CHONDRICHTHYES: BATOIDEA) FROM THE
TURONIAN (CRETACEOUS) OF MOROCCO

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Abstract. A new fossil batoid (ray) *Ptychotrygon rostrispatula* sp. nov. is described from five exceptionally well-preserved, three-dimensional skeletal remains from the Turonian (Late Cretaceous) of Morocco. These specimens represent the first known skeletal remains for the genus *Ptychotrygon* and allow an almost complete description of the genus providing a new insight to its phylogenetic relations and validate its taxonomic status as a member of the Sclerorhynchoidei. Mechanical preparation of the fossil remains revealed a relatively large batoid species (estimated total length beyond 1 meter). Overall morphology resembles that of sclerorhynchoids with a robust hypertrophied rostrum that lacks enlarged rostral denticles with enlarged paddle-like pectoral proximal elements (propterygium, mesopterygium and metapterygium). Never seen before details of the branchial skeleton are presented (large second hypobranchial without anterior process which was probably fused to the basibranchial and no evidence of articulation with other branchial element). To assess the phylogenetic relations of these specimens within the sclerorhynchoids a parsimonious analysis using TNT and PAUP software packages was performed. These analyses included *Asflapristis cristadentis* that along with *Ptychotrygon rostrispatula* sp. nov. were used as representatives of Ptychotrygonidae and also includes six other genera of sclerorhynchoids with relatively good skeletal remains. Both analyses recovered two monophyletic groups within sclerorhynchoids: the first contains *Ischyrhiza*, *Onchopristis* and *Schizorhiza* and a second that includes *Micropristis*, *Sclerorhynchus*, *Libanopristis* and Ptychotrygonidae.

Key words. Ptychotrygonidae, *Ptychotrygon rostrispatula*, sclerorhynchoids, phylogenetic, Cretaceous, Morocco.

SCLERORHYNCHOIDEI (*sensu* Cappetta 2012) is one of the most diverse group of extinct batoids, partly because they are easily recognised by their large rostral denticles. They are a

common element of shallow marine nearshore and non-marine Cretaceous assemblages of the Tethyan realm and the Western Interior Seaway (Becker *et al.* 2006), and some rarer forms such as *Ganopristis*, seem to have inhabited more Boreal and deeper waters (Underwood 2006).

It has been hypothesised that sclerorhynchoids occupied an ecological niche equivalent to that presently filled by large, shallow marine and non-marine species of sawfishes and smaller deeper water species of sawsharks (Welton & Farish 1993).

The group has been largely collected in localities of North America (Canada, USA, Mexico), Europe, Africa and the Middle East. Some of these localities, especially those of the Near East, have provided some beautifully well-preserved rostral blades and articulated skeletons of several genera: *Sclerorhynchus*, *Micropristis*, *Libanopristis*, *Ischyrrhiza* and *Schizorhiza* (e.g. Cappetta 1980; Sternes & Shimada 2018). Sclerorhynchoids had a peculiar morphology, including a hypertrophied rostrum with rostral denticles, antorbital cartilages not attached directly to the propterygium, a long synarcual that extended back to the scapulocoracoid with dorsally directed lateral stays and large pectoral pterygia elements (propterygium, mesopterygium and metapterygium) forming a solid structure with no pectoral radials directly articulated with the scapulocoracoid between them.

Despite what has been published about the skeletal anatomy of sclerorhynchoids, most of the fossil record of sclerorhynchoids, as with other chondrichthyans, is composed of highly mineralised skeletal elements (e.g. rostral cartilages and vertebral centra), and by regularly shed body elements with enamel layers (teeth, placoid scales, rostral denticles and tail spines). These structures are taxonomically informative enough to allow association for the group. However, in most cases the lack of one of these elements signifies taxonomic uncertainty. This is the case for several the taxa within sclerorhynchoids, *Ptychotrygon* being one of them, in which the lack of direct association to rostral denticles has led to taxonomic uncertainty for the genus.

Ptychotrygon taxonomic affiliations have changed from group to group since its redescription, from *Ptychodus triangularis* (von Reuss, 1844) to *Ptychotrygon triangularis* by Jaekel (1894) based on new specimens from the Kreideformation (Turonian) in Bohemia. McNulty & Slaughter (1972), placed the genus within the batoids in the family Dasyatidae and suggested that the tooth morphology fits as part of the galeoid-batoid succession, along

with its similarities with other sclerorhynchoids (ganopristoid). Cappetta (1973) retained the dasyatoid affiliation, however based on histological features of teeth mentioned its possible affiliation with Rajiformes. Cappetta & Case (1999) based on Cappetta's (1973) observations placed the genus as either a sclerorhynchoid or a rhinobatoid, due to the lack of direct association between rostral denticles and oral teeth. Kriwet (1999) placed it within the Rajiformes, based on the resemblance of the possible rostral denticles found in mixed assemblages with those of Rajidae, and also mentioned their similarity with those of other sclerorhynchoids found in other fossil assemblages (e.g. Case 1978). Large dermal denticles, similar to those reported by Kriwet (1999) have been observed for *Libanopristis hiram* (pers. observations) and described for *Sclerorhynchus atavus* (Welten *et al.* 2015, Underwood *et al.* 2016). Cappetta (2006) placed *Ptychotrygon* within the Rajiformes with its more exclusive taxonomic affiliations uncertain, as still no direct association with rostral denticles has been found. Kriwet *et al.* (2009) placed the genus within the order Sclerorhynchiiformes (*sensu* Kriwet 2004) and based on its teeth morphology proposed the family Ptychotrygonidae. Cappetta (2012) kept the family Ptychotrygonidae which included three genus *Ptychotrygon*, *Ptychotrygonoides* and *Texatrygon*. However, the systematic affiliation and position of the genus and family with the sclerorhynchoids remained doubtful as no direct association between rostral denticles and teeth has been proven.

Recently several extremely well-preserved three-dimensional remains of sclerorhynchoids with previously unseen morphological details have been discovered in the region of Asfla in the northeast of Morocco corresponding to the Late Cretaceous, allowing a restudy of the phylogenetic relations and taxonomic classification of this genus. Of these specimens five present a similar tooth morphology to *Ptychotrygon* providing the first skeletal record for this genus and six present a previously unknown morphology that belongs to a new species and genus *Asflapristis cristadentis* Villalobos *et al.* (2019). These specimens are included in a phylogenetic analysis along with several other species of sclerorhynchoids trying to recover a phylogenetic topology for the sclerorhynchoids.

GEOLOGICAL SETTING

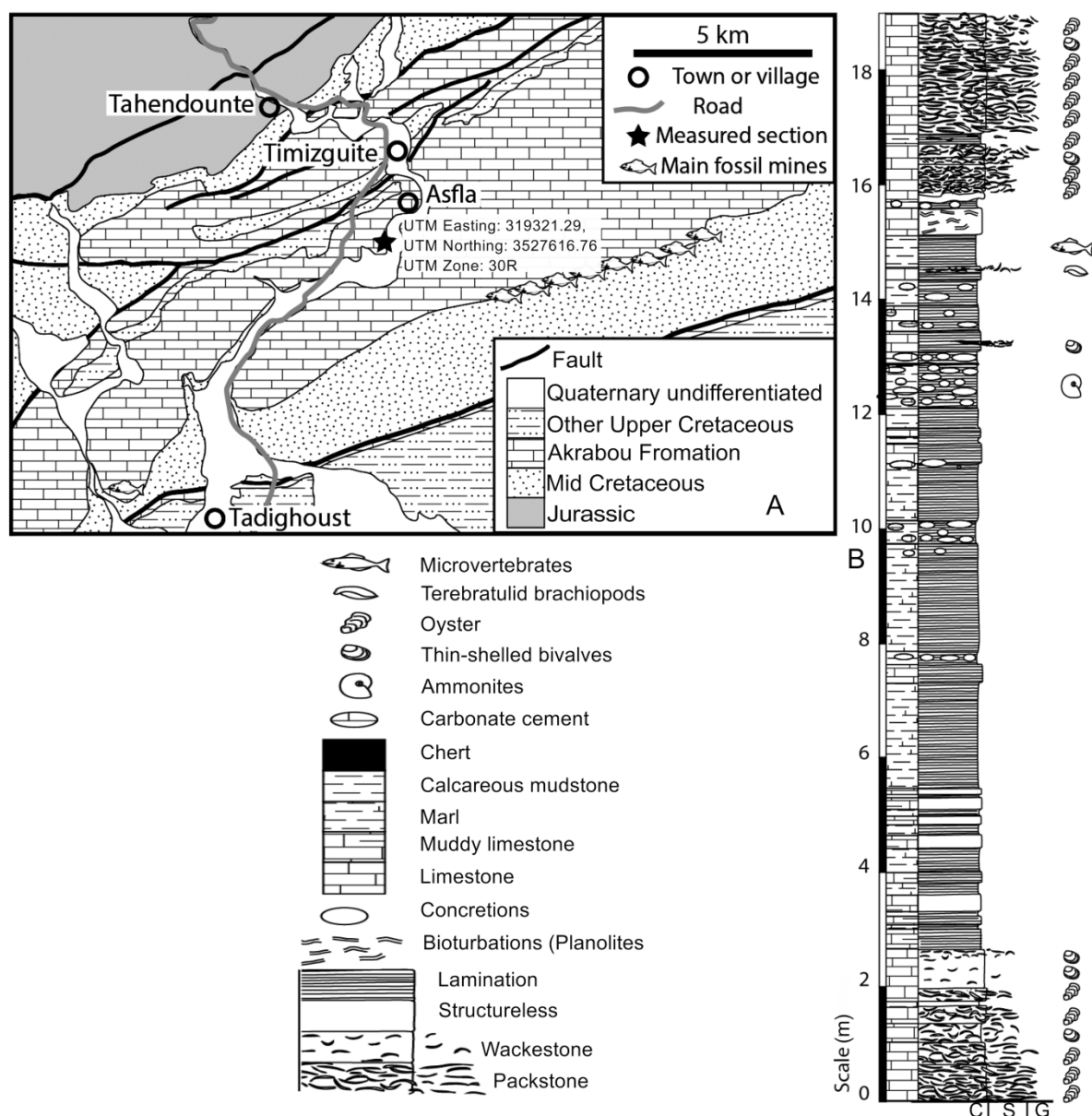


FIG. 1. A, Locality map; B, Stratigraphic column of the Turonian in Asfla. Coordinates in figure A correspond to the measured section (UTM Easting: 319321.29, UTM Northing: 3527616.76 and UTM Zone: 30R).

A short account of the geological setting of the area is presented here, for a more detailed description see Villalobos *et al.* (2019). All specimens described here come from Asfla, an area north of the town of Goulmima, southeast Morocco (Fig. 1), that is well known for fossils of ammonites (e.g. Cavin *et al.* 2010; Kennedy *et al.* 2008) and vertebrates (e.g. Ettachfini & Andreu 2004). The locality corresponds to the Akrabou Formation, a unit of late Cenomanian to Turonian (Cretaceous) age, that overlies the famously fossiliferous ‘mid’ Cretaceous ‘Kem Kem’ fluvial facies and is overlain by further non-marine late Cretaceous

rocks suggesting a strongly transgressive succession and relatively high sea-level, followed by a regressive episode.

At this site fossils are generally enclosed in ovoid concretions between 0.2-0.3 metres long, that typically take on the general shape of the enclosed fossil. Batoid and teleost skeletons collected from the area are three dimensionally preserved, with skeletal elements occupying several planes within the concretion (Cavin *et al.* 2010), although there may be some crushing of larger elements (Claeson *et al.* 2013). Soft tissue preservation has been recognised in one specimen of *Ptychotrygon rostrispatula* sp. nov. (holotype), and phosphatised muscle tissue was noted in another batoid taxon (Claeson *et al.* 2013). This, albeit rare, preservation of soft tissue points towards a hostile seafloor environment with poor conditions for decomposing organisms (Lezin *et al.* 2012); microbially-mediated precipitation of apatite being more rapid than complete decay of soft tissues (Martill 1988). This is also supported by the infrequent benthic fossils seen in the site mostly composed of thin shelled bivalves (possible Lucinidae) and very small gastropods. Small cirripede plates and comatulid crinoids are common in some commercially obtained concretions, but their provenance is uncertain.

MATERIAL AND METHODS

All specimens were obtained from Morocco-based commercial sources, either from fossil collectors in Goulmima itself or from larger scale local wholesalers based in Erfoud, Rissani and Rich. Specimens were either partially or completely prepared. In all cases some cartilage with tesserae was showing on the surface of the nodule. The concretions enclosing the batoid remains are very hard, whilst cartilage elements are often fragile, and tesserae are commonly slightly disarticulated similar to those reported for the Santana formation Brazil (Martill 1988; Brito & Steret 1998; Brito *et al.* 2013) The somewhat shattered tesserae ruled out acid preparation of the specimens, and mechanical preparation was only carried out when necessary, to potentially expose characters not seen elsewhere. Mechanical preparations were performed in the Natural History Museum of the United Kingdom (NHMUK), where the fossil material is currently housed.

For the study of microvertebrates remains, approximately 125 kilograms of the surrounding marl matrices were sieved, using a series of sieves down to a 0.375mm mesh. Residues were

treated in 7.5% formic acid buffered with calcium formate (spent acid) at a pH of 3.2 or above to remove carbonate fragments and yielded abundant teeth of *Ptychotrygon rostrispatula* sp. nov. along with extremely small teeth resembling those of *Rhinobatos*.

A matrix of 14 taxa and 23 characters (<https://doi.org/10.5061/dryad.2t8c60f/1>) using new observations and characters from (Aschliman *et al.* 2012; Claeson *et al.* 2013; Underwood & Claeson 2017) was assembled in Mesquite 3.31 (Maddison 2008) using contingent/reductive coding (Brazeau 2011), as spurious results can arise from this coding referring to zero-length branches (ZLB) (Strong & Lipscomb 1999). The ZLB were collapsed, this is done by default in NONA and TNT and has to be set manually in PAUP (Brazeau 2011). Fast and slow optimisations were used to evaluate all mapping possibilities and character state changes implications.

The matrix includes eight sclerorhynchoid taxa with relatively good skeletal remains. Following Villalobos *et al.* (2019), the outgroups included three members of Rajidae (*Amblyraja radiata*, *Raja clavata* and *Rajella fyllale*), a Jurassic batoid (*Spathobatis bugesicus*) and three members of Rhinopristiformes (*Rhinobatos glaucostigma*, *Anoxypristis cuspidata* and *Pristis* sp.). The matrix was analysed in the phylogenetic software TNT 1.1 (Goloboff *et al.* 2008) and PAUP 4.0 (Swofford 2003). As TNT was conceived mostly as a tool for analysis of large data sets, we contrast its result with those of PAUP and characters were mapped and optimized using WINCLADA (Nixon 2002).

In both, the TNT and PAUP analyses a heuristic search with unweighted characters was performed. The TNT search was performed with the menu interface and the following parameters: tree bisection and reconnection (TBR) was used as the search algorithm, 1000 random seed, 10000 replications and 10 trees saved per replication, followed by an exhaustive search in PAUP. The PAUP search used the heuristic option with TBR as search algorithm and stepwise addition with 1000 random replications. The Bootstrap analysis was performed in PAUP with 1000 iterations of random stepwise addition, to evaluate the support for all the clades recovered by the heuristic and total evidence analyses (<https://doi.org/10.5061/dryad.2t8c60f/2>). The analyses kept two uninformative characters (chars. 3 and 10); due to the lack of information they currently do not provide group data, however, they may offer interesting discussion points for future works (see character discussion).

Material examined. *Amblyraja radiata*, BRC-Amblyraja. *Anoxypristis cuspidate*, A.442.6. *Asflapristis cristadentis*, NHMUK PV P 73925, 75428 a-e, 75429 a-d, 75431, 75432, 75433. *Ischyrhiza mira*, Sternes & Shimada (2018, text-fig. 2 a-I, text-fig. 4 a-f, text-fig. 5 a-i); Slaughter & Steiner, (1968, text-fig. 4A-C). *Micropristis solomonis*, Cappetta (1980, pl. 1, fig. 1-4; pl. 2, fig. 1). *Libanopristis hiram*, Cappetta (1980, pl. 1, fig. 4); NHMUK PV P 108705, 108706, 13858, 63610, 75075. *Onchopristis numidus*, NHMUK PV P 75502, 75503. *Ptychotrygon rostrispatula* sp. nov., NHMUK PV P73630, 75496, 75496, 75497, 75500. *Pristis* sp., BRC-Pristis. *Raja clavata* BRC-Raja. *Rajella fyllale* BRC-Rajella. *Rhinobatos glaucostigma*, CNPE-IBUNAM 17810, *Sclerorhynchus atavus*, Slaughter & Steiner (1968, text-fig. 4D); NHMUK PV P4017, 4776, 49546, 49518, 49533, 49547. *Shizorhiza stromeri*, Smith *et al.* (2015, text-fig. 1a-l; 2a-f); NHMUK PV P 73625. *Spathobatis bugesicus*, NHMUK P6010, 2099 (2); BSP AS I 505, 1952 I 82. *Zapteryx brevirostris*, UERJ 1234, 1237, 1240.

Institutional abbreviations. A, Royal College of Surgeons, London (Hunterian Museum) BRC: Birkbeck Reference Collection. BSP: Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany. NHMUK: Natural History Museum United Kingdom, London. UERJ: Universidade do Estado do Rio de Janeiro

SYSTEMATIC PALAEONTOLOGY

CHONDRICHTHYES Huxley, 1880
 BATOMORPHII Cappetta, 1980
 RAJIFORMES Berg, 1940
 SCLERORHYNCHOIDEI Cappetta, 1980
 PTYCHOTRYGONIDAE Kriwet *et al.*, 2009
 Genus *Ptychotrygon* Jaekel, 1894

Type species. *Ptychotrygon triangularis* (von Reuss, 1844)

Diagnosis. Hypertrophied rostrum with no enlarged denticle series attached to it and with two parallel ventral canals, one on each side of the rostrum. Palatoquadrate and Meckel's cartilages slim. Second and third hypobranchials well-developed, close to each other and with no articulation surface with the basibranchial. Teeth are small and oval-shaped, with a sharpened, strong enamelled pyramidal crown and transverse crests (in some cases short transverse ridges are present on the labial crown face). Labial apron variably developed and

in some cases with a straight sagittal ridge on the upper part. The apron is bent basally with a truncated projection. The lingual uvula is short and broad with central interlocking depression. In profile view, the labial face is sigmoidal. Root of holoaulacorrhizous type with a single pair of margino-lingual foramina.

Ptychotrygon rostrispatula sp. nov.
LSID. urn:lsid:zoobank.org:act:XXXXXXXXXX
Figures 2-7

Synonymy: Holotype specimen was first illustrated in Underwood *et al.* (2016, text-fig. 3a)

Diagnosis.

Homologous characters: Sclerorhynchoid batoid with estimated total length (TL) well in to more than one metre. Hypertrophied rostrum (31% of total preserved length in holotype specimen), that reaches maximum width away from the base giving it a leaf shape. No enlarged rostral denticles associated to the rostrum were observed. Chondrocranium rectangular-shaped, reaches its maximum width at the nasal capsules and posterior to this region becomes narrower. Chondrocranium roof flattened. Palatoquadrate and Meckel's antimeres are separated and slender. Dentition relatively homodont, teeth oval in occlusal view and present two well-developed transversal crests, with a variably developed medial cusp between them. Labial visor and lingual uvulae variably developed. Root low with widely spaced root lobes with rounded and flat basal face. Second hypobranchial long and pillar shaped, without an anterior process and no articulation surface with the basibranchial. Ventral portion of the scapulocoracoid is narrow and bar-like, the lateral facet of scapulocoracoid is compact and articulates to the distally expanded and paddle-like proximal pectoral elements (Propterygium, Mesopterygium and Metapterygium). The mesopterygium is square shaped and lack of any process. All pectoral radials articulate directly with the proximal element of the pectoral fin. Pelvic girdle slender and bar like without any process.

Autapomorphy characters: Narrow but well-developed labial apron. Transversal crest on labial edge steeps towards the middle crests. Distal edge of labial apron slightly convex.

Derivation of species name. Making reference to the presence of the flat and hypertrophied rostrum.

Holotype. NHMUK PV P 73630, almost complete specimen with only the right pectoral fin, pelvic and caudal fin missing and the ventral surface exposed.

Paratypes. NHMUK PV P 75496, almost complete male specimen, with most of the ventral surface and proximal part of the left clasper exposed. The appendicular skeleton (pectoral and pelvic fins) are missing along with the pelvic girdle and dorsal and caudal fin. NHMUK PV P 75498, almost complete juvenile specimen with the dorsal surface of the synsacral, neurocranium and part of the pectoral girdle exposed after preparation. In the posterior region of the specimen a tooth was found that allowed its identification. NHMUK PV P 75497, an incomplete specimen that preserves the rostrum, neurocranium and part of the jaw, with the ventral surface exposed. Part of the lower jaw was prepared and revealed a single tooth. NHMUK PV P 75500, fragmented specimen with only the ventral surface of the branchial skeleton and parts of the jaw cartilages with teeth preserved.

Stratigraphical and geographical provenance. Specimens occurrences correspond to the high escarpments of the Akraou Formation south and east of Asfla. Coordinates of those escarpments are given in Universal Transverse Mercator units (UTM) (UTM Easting: 319321.29, UTM Northing: 3527616.76, UTM Zone: 30R). These localities contain a diverse ammonite fauna (Kennedy *et al.* 2008) indicative of the *Mammites nodosoides* biozone of the early Turonian (Cavin & Dutheil 1999).

Description

Chondroskeleton. The exposed skeletal elements show a sclerorhynchoid body-shape, with several characteristic features of the group (e.g. hypertrophied rostrum, paddle-like pectoral elements and lack of articulation surface between second hypobranchials and basibranchial) (Fig. 2). All skeletal elements are formed by a layer of small of prismatic calcified cartilage blocks. Unlike *Asflapristis* the palatoquadrate and Meckel's cartilage of *Ptychotrygon rostrispatula* sp. nov. lack the external layer of fibrous cartilage that resembles wood cortex with several vertical, parallel and well mineralized ridges, henceforth "wood-like cartilage".

Chondrocranium. Box-shaped structure, reaching its maximum width at the nasal capsules and its minimum at the orbital region. The nasal capsules are oval shaped, slightly anteriorly directed and laterally expanded with a flat anterior edge. The antorbital cartilages are

connected to the nasal capsules and have a crescent shape with smooth margins and project posterolaterally, with its acute tip directed towards the pectoral fins. In dorsal view the supraorbital crests are flatted and at the same level of the rest of the chondrocranium, but this could be the result of dorsoventral deformation. The posterior edge of the chondrocranium is exposed and presents a deep cavity for the insertion of the odontoid process (synarcual lip) and large occipital condyles that project laterally.

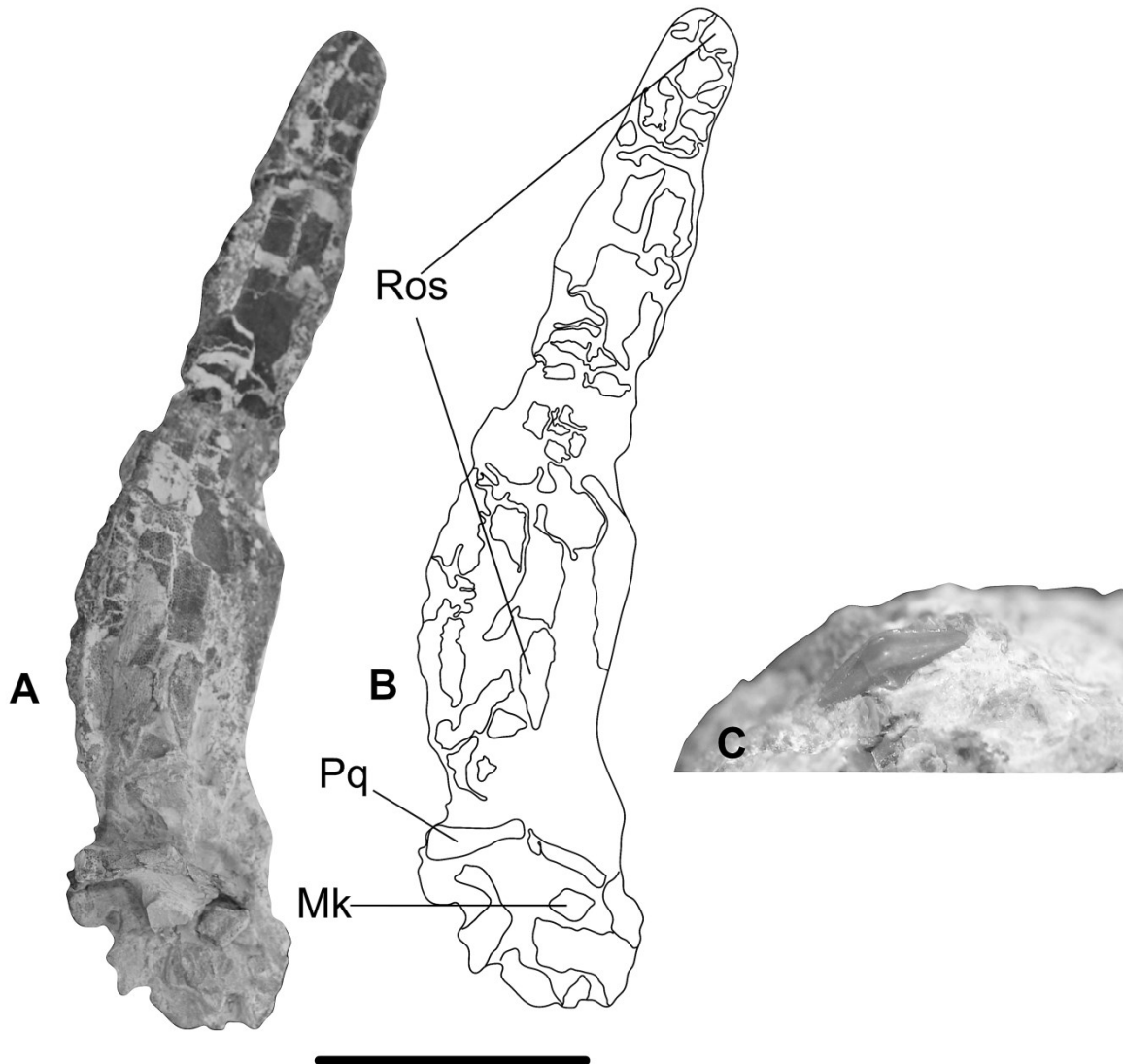


FIG. 2. *Ptychotrygon rostrispatula* sp. nov. NHMUK PV P 75497. A, Ventral surface of rostral cartilages. B, Interpretative drawing. C, teeth. *Abbreviations:* mk, Meckel's cartilage; pq, palatoquadrate; ros, rostrum. (scale bar: 10 cm).

Rostrum. Fragile and thin. Hypertrophied extending well-beyond the chondrocranium (Fig. 2), reaches its maximum width well before the base giving it a leaf shape. Ventral surface

with two parallel deep grooves that run all the way from the base of the rostrum to the tip (Fig. 3), it for the buccopharyngeal nerve as in other sclerorhynchoid species (Kriwet 2004). No evidence of rostral denticles directly associated with it was observed.

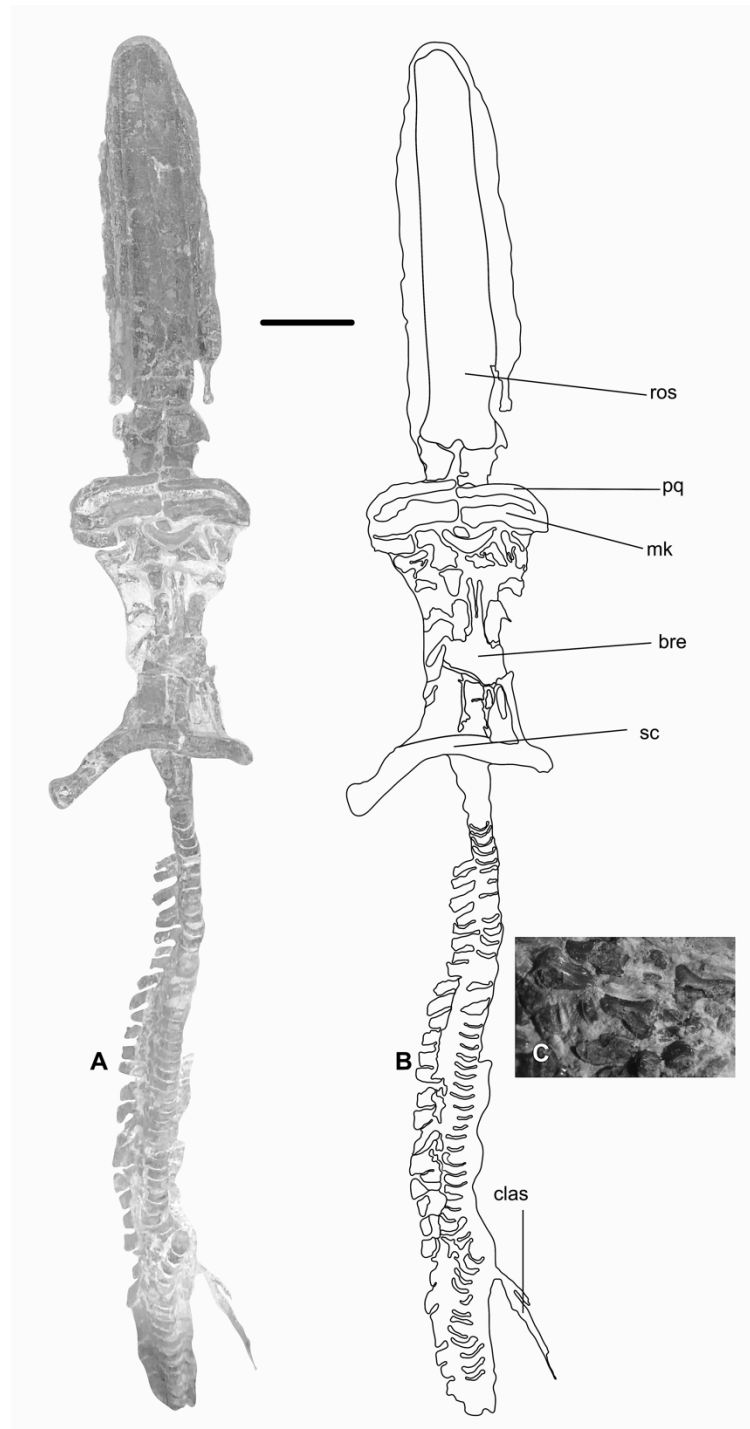


FIG. 3. *Ptychotrygon rostrispatula* sp. nov. NHMUK PV P 75496. A, ventral surface of axial and part of appendicular skeleton. B, Interpretative drawing. C, teeth. *Abbreviations:*

brE, branchial elements; clas, clasper; mk, Meckel's cartilage; pq, palatoquadrate; ros, rostrum; sc, scapulocoracoid. (scale bar: 5 cm).

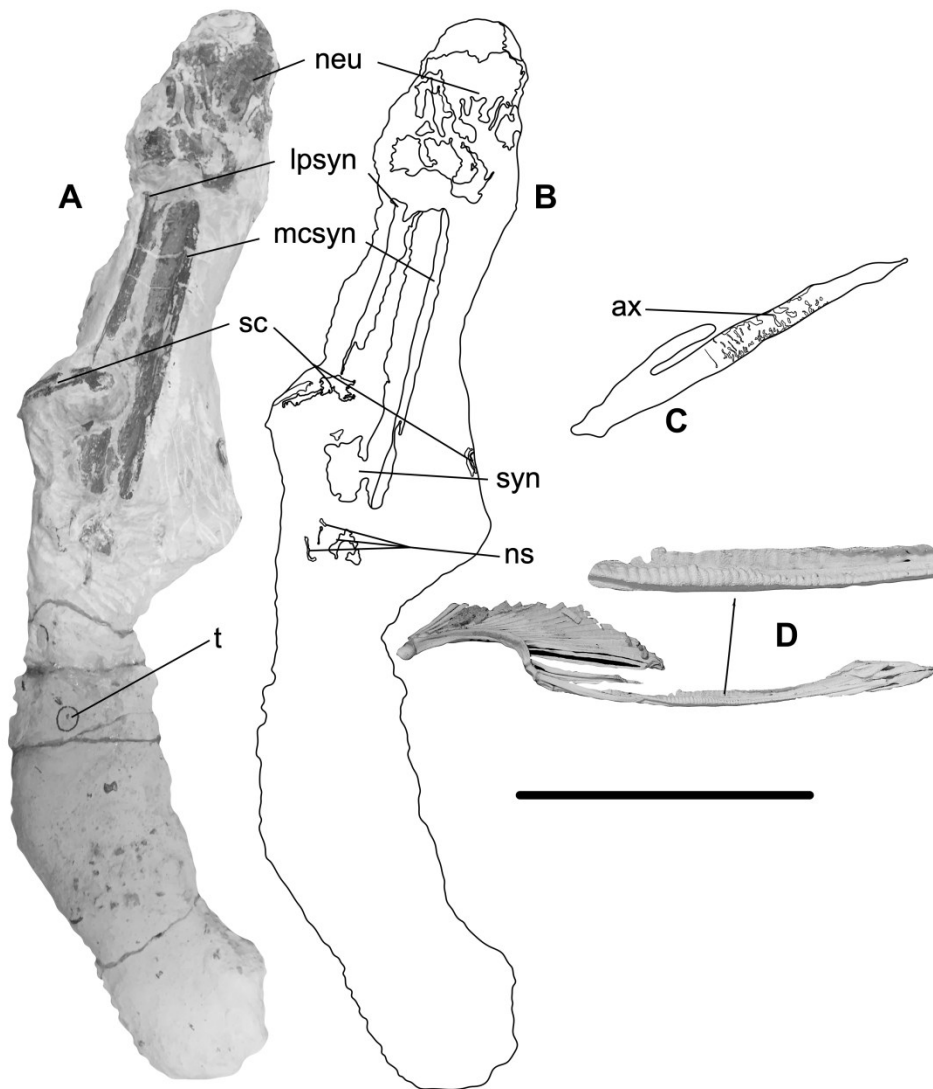


FIG. 4. *Ptychotrygon rostrispatula* sp. nov. NHMUK PV P75498. A, Dorsal surface of axial skeleton. B, Interpretative drawing. C, Clasper details of NHMUK PV 75496. D, Clasper and clasper's axial cartilage of *Zapteryx brevirostris* UERJ 1240. *Abbreviations:* ax, axial cartilage; lpsyn, lateral process of synarcual; mcsyn, medial crest of synarcual; neu, neurocranium; ns, neural spines; sc, scapulocoracoid; syn, synarcual; t, teeth. (scale bar: 10 cm).

Synarcual, axial skeleton and claspers. The synarcual cartilage is long and surpasses the scapulocoracoid. It narrows after the anterior lateral articular facets that project laterally. These facets are attached to a deep groove on the posterior portion of the neurocranium

suggesting a tight interaction between them and a rigid structure. After one third its length the synarcual progressively widens until reaching its maximum width behind its middle point (Figs. 4A-B). The medial crest of the synarcual is well-developed and projects dorsally (Figs. 4A-B). In ventral view the vertebral centra fail to reach the middle of the synarcual.

Several thoracic and caudal vertebrae are preserved and show a dense notochordal centrum with appositional rings of areolar cartilage, which are consistent with the episodic growth rings seen in other elasmobranchs.

Only a portion of the axial cartilage of the left clasper is preserved. This cartilage is ribbed (Fig. 4C), similar to that of *Kimmerobatis* Underwood & Claeson, 2017 and *Zapteryx brevirostris* (Müller & Henle, 1841) (Fig. 4D)

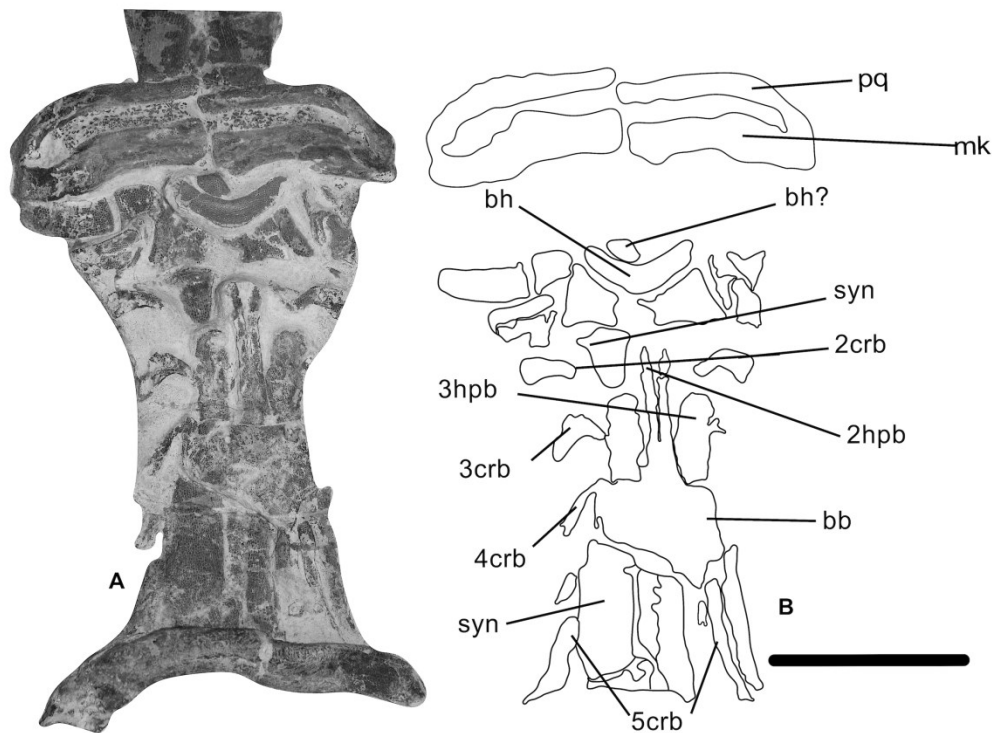


FIG. 5. *Ptychotrygon rostrispatula* sp. nov. NHMUK PV P75496. A, Ventral view of visceral skeleton (mouth and branchial). B, Interpretative drawing. *Abbreviations:* mk, Meckel's cartilage; pq, palatoquadrate. bh, basihyal; bb, basibranchial; 2crb, second ceratobranchial; 3crb, third ceratobranchial; 4crb, fourth ceratobranchial; 5crb, fifth ceratobranchial; 2hpb, second hypobranchial; 3hpb, third hypobranchial. (scale bar: 5 cm).

Visceral Skeleton. No labial cartilages were observed. The mouth cavity is large. The paired Meckel's and palatoquadrate cartilages are straight and slender (Fig. 5A). There is damage on the posterior surface of the Meckel's cartilage in the holotype (NHMUK PV P73630) and paratype (NHMUK PV P 75496) but there seems to have been a socket for articulation with the palatoquadrate. The hyomandibula is triangular shaped, with its acute distal edge facing the Meckel's cartilage and its wide posterior edge is directed towards the otic region of the chondrocranium.

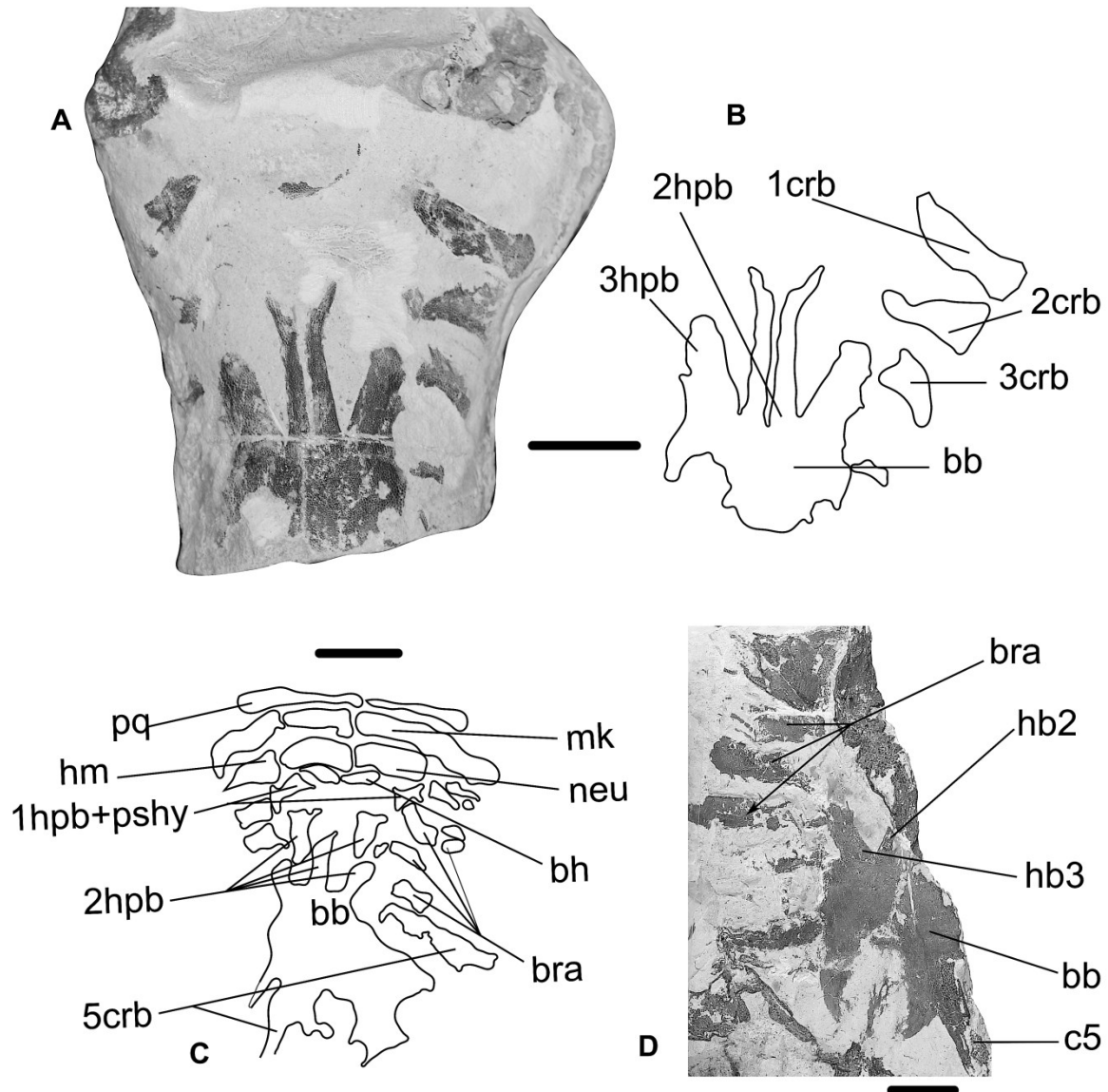


FIG. 6. A-C, Ventral view and interpretative drawing of branchial skeletons of *Ptychotrygon rostrispatula* sp. nov. NHMUK PV P 75500 (A-B. scale bar: 5 cm). C, Interpretative drawing of NHMUK PV P 73630 (scale bar: 4cm). D, branchial skeletons of *Sclerorhynchus atavus* NHMUK PV P 49546 (scale bar: 1cm). *Abbreviations:* bb, basibranchial; bh, basihyal; bra, branchial elements; 1crb, first ceratobranchial; 2crb, second

ceratobranchial; 3crb, third ceratobranchial; 4crb, fourth ceratobranchial; 5crb, fifth ceratobranchial; 1hpb, first hypobranchial; 2hpb, second hypobranchial; 3hpb, third hypobranchial; hm, hyomandibula; mk, Meckel's cartilages; pq, palatoquadrate; pshy, pseudohyal.

The branchial cartilages are thick and well mineralised. The basihyal is wide, crescent shaped and fragmented in two parts; it is located behind the neurocranium and under the synarcual (Figs. 5-6A-C). The basihyal and first hypobranchial are disarticulated as a result of the fossilisation process (Figs. 6C). The first hypobranchial is T-shaped with regular edges and with its wide edge (distal end) facing the pseudohyal (Fig. 6C). The fork-like anterior processes that project from the basibranchial are the second and third hypobranchials, which present a similar configuration to modern rajoids and *Sclerorhynchus atavus* (Fig. 6D). At least two ceratobranchial cartilages articulate with the third hypobranchial and there is no evidence of articulation between the ceratobranchials and second hypobranchial. The fourth to fifth ceratobranchials are directed towards the scapulocoracoid and at least the fifth ceratobranchial reaches the scapulocoracoid (Fig. 4 and 5C). The basibranchial and base of the fifth hypobranchial could be distinguished from each other.

Appendicular skeleton. The scapular process projects dorsally, whether the process was long or short is unknown. Ventrally the scapulocoracoid is straight and bar-like. The lateral facet of the scapulocoracoid is compact and square shaped, with no direct articulation with the pectoral radials scapulocoracoid (Fig. 7A-C). There are three pectoral condyles (procondyle, mesocondyle and metacondyle) for the articulation of the proximal pectoral elements (propterygium, mesopterygium and metapterygium). The proximal pectoral elements are sturdy and paddle-like: the propterygium anterior process is missing and its posterior section does not extend behind the procondyle (Fig. 7C), the preserved portion in the holotype supports 12 pectoral radials on its distal edge. The mesopterygium is trapezoid shaped and narrower than the rest of the proximal elements with eight pectoral radials connected to its distal edge. The metapterygium is long, curved and directed towards the tail and supports 27 pectoral radials. It is uncertain if the paired fins were aplestodic or plesodic as only the first series of pectoral radials is preserved, however, the condition in all other known fossils of sclerorhynchids is plesodic. Most of the pelvic skeleton is missing, only the ventral face of the puboischiadic bar is exposed, which is narrow, plate like with smooth edges and slightly arched in the middle (Fig. 7).

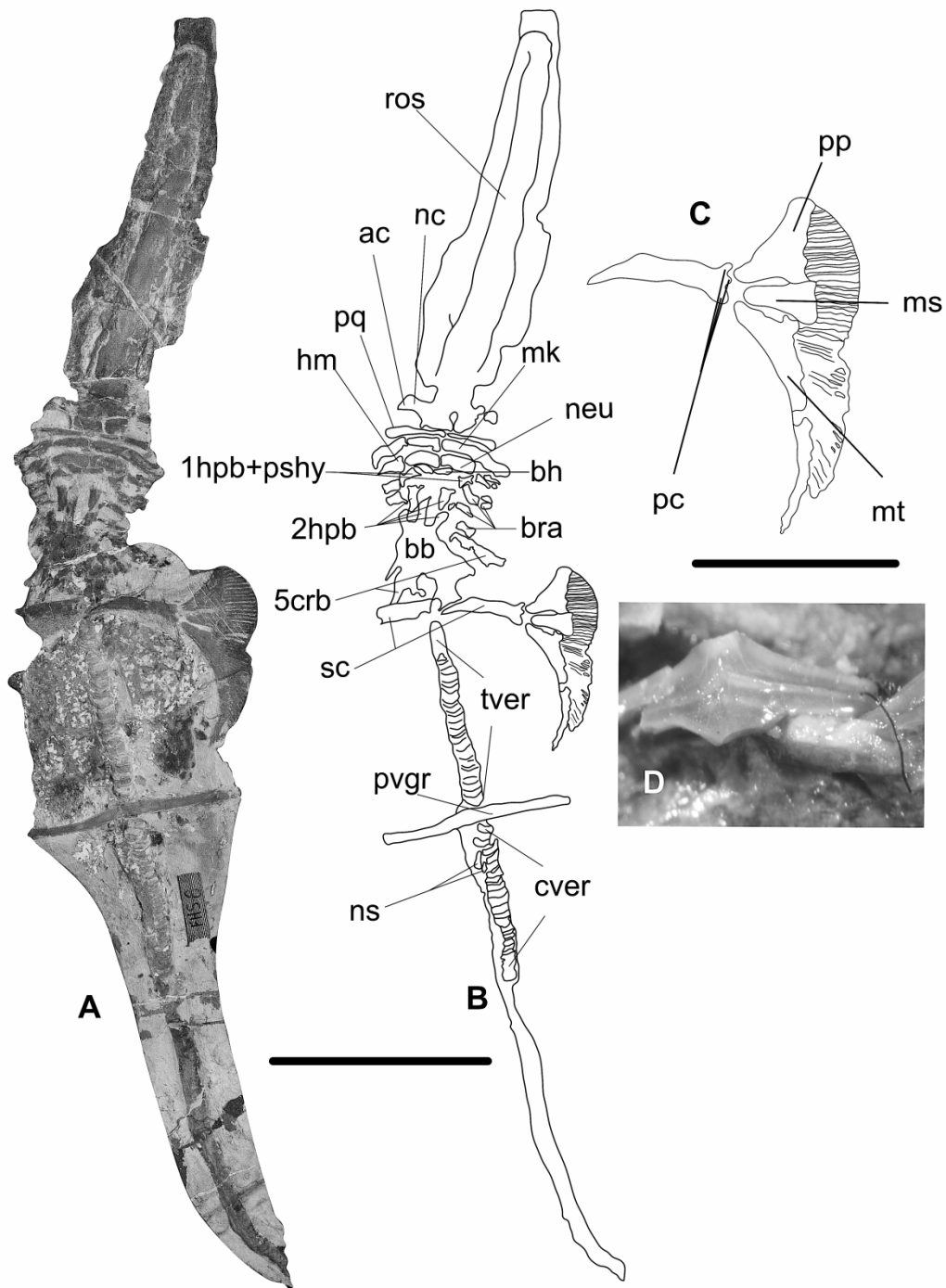


FIG. 7. *Ptychotrygon rostrispatula* sp. nov. NHMUK PV P73630 (holotype). A-B ventral surface of specimen (scale bar: 20 cm). C pectoral fin (scale bar: 10 cm). D, teeth. *Abbreviations:* ac, antorbital cartilage; bb, basibranchial; bh, basihyal; bra, branchial elements; 5crb, fifth ceratobranchial; cver, caudal vertebrae; hm, hyomandibula; 1hpb; first hypobranchial; 2hpb, second hypobranchial; mk, Meckel's cartilages; ms, mesopterygium; mt, metapterygium; nc, nasal capsules; neu, neurocranium; ns, neural spines; pc, pectoral

condyles; pp; propterygium; pq, palatoquadrate; pshy, pseudohyal; pvgr; Pelvic gridle; ros, rostrum; dc, scapulocoracoid; tver, thoracic vertebrae.

Teeth. Descriptive tooth terminology follows that of Cappetta (1987). The dentition is relatively homodont, with some variation in tooth size. The teeth are gracile (up to 2 millimetres (mm) wide) and generally oval-shaped, slightly expanded labially. In dorsal view, tooth crown surpasses the root on all sides (Fig. 8), with strong enamelled: medial crest and transverse crests on the labial and lingual sides (Figs. 8A-B, G-H). The medial crest is pyramidal shaped, and its development varies among teeth. The transverse crest on the apron labial is generally well-developed and steeps in the middle towards the medial crest. Smaller ridges at the base of the labial apron extending towards the middle of the labial face are also present (Figs. 8D, I, L). In lingual view, there is a small lingual uvula, with a central interlocking depression, that connects with the lingual transverse crest (Figs. 8 E-F, K-L). On lateral view the apron projects anteriorly and the ligula profile is slightly sigmoidal (Fig. 8M). The roots are bilobed, and the lobes are equal sized and rounded. The basal faces of the root lobes are convex and there is no sharp edge between the lateral and basal faces (Fig. 8N).

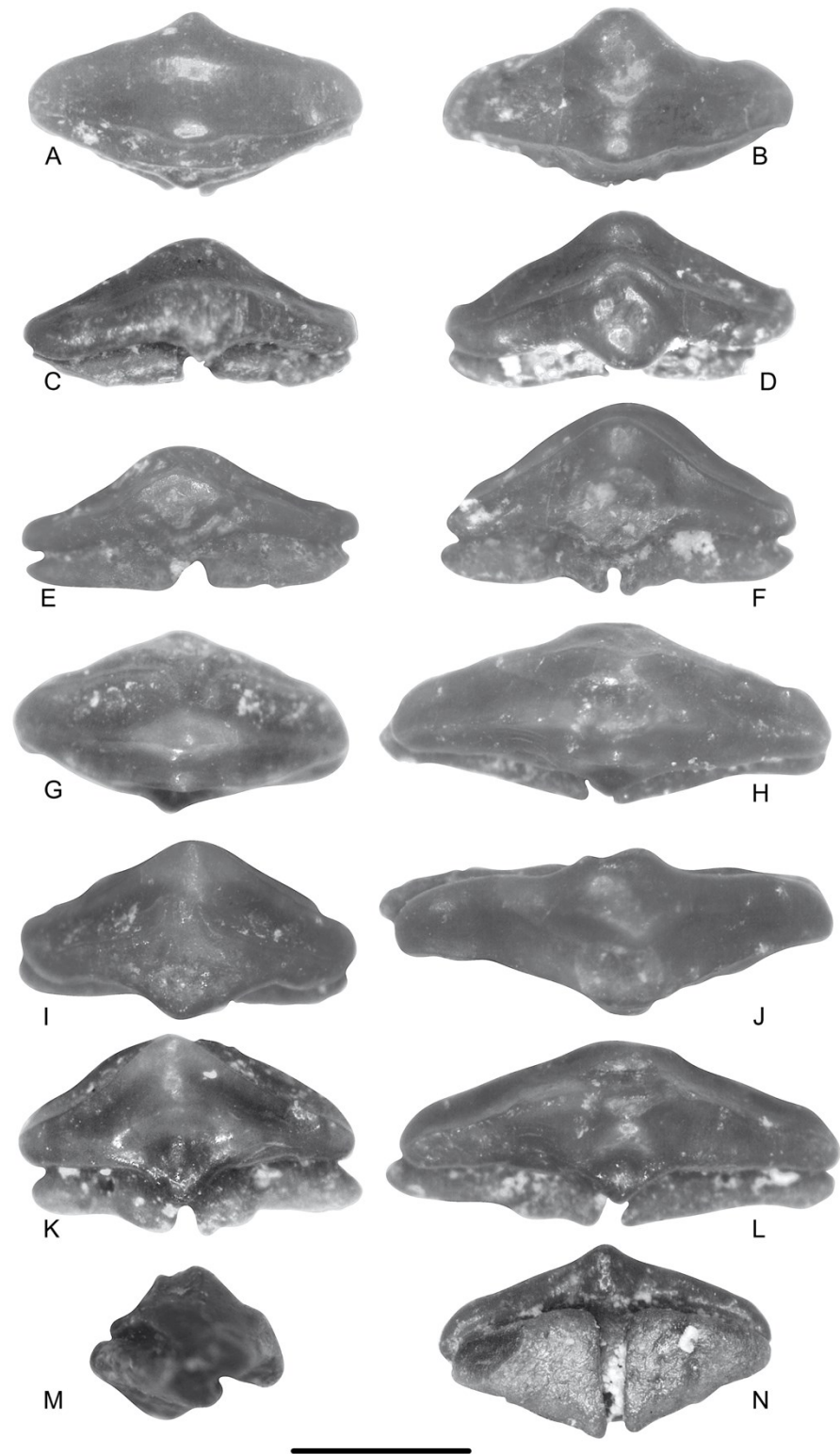


FIG 8. Teeth of *Ptychotrygon rostrispatula* sp. nov. A-B and G-H, occlusal view. C-D and I-J, labial face. E-F and K-L, lingual face. M, profile. N, root. (scale bar: 2 mm).

Based on Kriwet *et al.* (2009) the specimens of *Ptychotrygon rostrispatula* sp. nov. were assigned to the genus *Ptychotrygon* by the presence of the following characters: teeth small; tooth crowns broader than long; crown with subtriangular outline in occlusal view and with more or less well-developed transversal crests on the labial face (number of transversal crests varying), the presence of a well-developed labial apron and lingual uvula short and broad with central interlocking depression. It is worth mentioning that the presence of transverse crests on the labial apron has been reported for *Libanopristsis* (Cappetta 1980, text-fig. 7 B; 2012, text-fig. 368 I), However, in general the teeth of *Libanopristsis* present more prominent cusp and the labial apron less ornamented than those of *Ptychotrygon* (Fig. 9). The lingual uvula in *Ptychotrygon* presents a deep central interlocking depression. Cappetta (1980) mentions this depression for some teeth of *Libanopristsis hiram* but it is not clear from the illustrations if it refers to the profile of lingual face or if it is referred to a region of the lingual uvula.

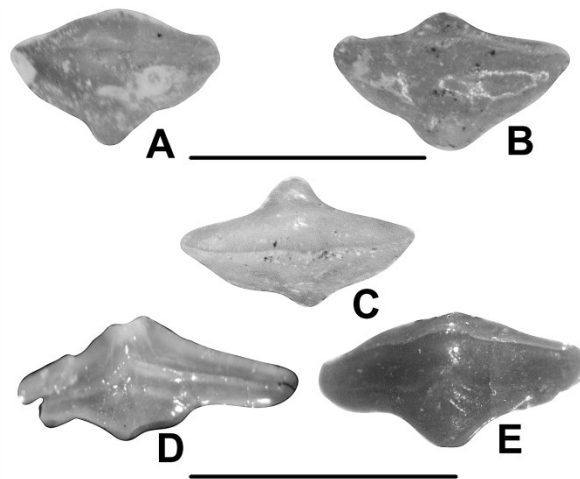


FIG 9. A-C, occlusal view of teeth of *Libanopristsis hiram* (NHMUK PV P 13858) (scale bar: 1 mm). Teeth of *Ptychotrygon rostrispatula* sp. nov. D, labial view and E, occlusal view (scale bar: 2 mm).

Ptychotrygon rostrispatula sp. nov. teeth ornamentation differs from other congeneric species of *Ptychotrygon* (Leriche, 1940; McNulty & Slaughter, 1972; Welton & Farris, 1993; Cappetta 2006 and 2012; Kirkland *et al.* 2013; Cicimurri *et al.* 2014)

P. boothi Case, 1987 lacks a concave lingual uvula and the steep mid portion of the transverse crest in labial apron.

P. henkeli Werner, 1989 lacks a labial transverse crest.

P. triangularis (von Reuss, 1844) presents a more ornamented labial apron with generally more than one transverse crest and a straight lingual profile.

P. agujaensis McNulty & Slaughter, 1972 and *P. chattahoocheensis* Case *et al.*, 2001 present more than one transverse crest on the labial apron all of which lack the steep mid portion.

P. blainensis Case, 1978 presents several branching ridges on the labial apron that extend from the cusp of the medial crest to the base of the crown and presents a straight lingual profile.

P. cuspidata Cappetta & Case, 1975a lacks transversal ridges and present a prominent medial cusp and several ridges restrained to its labial apron.

P. ellae Case, 1987 present a more developed lingual uvula that extends into the root, along with a much more prominent lingual transverse crest.

P. eutawensis Case *et al.*, 2001 presents a more ornamented labial apron with several longitudinal ridges reaching in to the transverse crest.

P. geyeri Kriwet, 1999 lacks transversal ridges and a more ornamented labial apron with several branching ridges.

P. pustulata Kriwet *et al.*, 2009 lacks the steep in the middle of the secondary crest towards the medial crest on the labial apron and presents conical ridges on the transverse and medial crests.

P. rugosa (Case *et al.*, 2001) presents a large labial apron with several transverse ridges and lack of a well-developed medial crest.

P. striata Kriwet *et al.*, 2009 presents a more ornamented labial face with several straight ridges some of which have a steep pattern and present a straight lingual profile.

P. texana (Leriche, 1940) presents a more ornamented labial face with several transverse crest which have a steep pattern and present a straight lingual profile.

P. ledouxii Cappetta, 1973, *P. slaughteri* Cappetta & Case, 1975b and *P. vermiculata* Cappetta, 1975 lacks the steep in the middle of the labial apron transverse crest towards the medial crest, and *P. winni* Case & Cappetta 1997 also by its concave lingual profile.

Ptychotrygon rostrispatula sp. nov. teeth bear resemblance to those of *Libanopristis hiram* (Cappetta 1980, text-fig. 7 B; 2012, text-fig. 368 I) and *Texatrygon* (Cappetta & Case, 1999) (Cappetta 2012, text-fig. 382 A-I). However, *Ptychotrygon rostrispatula* sp. nov. teeth

present a less prominent cusp and lingual uvula and a more ornamented labial apron with a transversal crest that steep in the middle towards the medial crest (Figs. 8D, 9E).

RESULTS

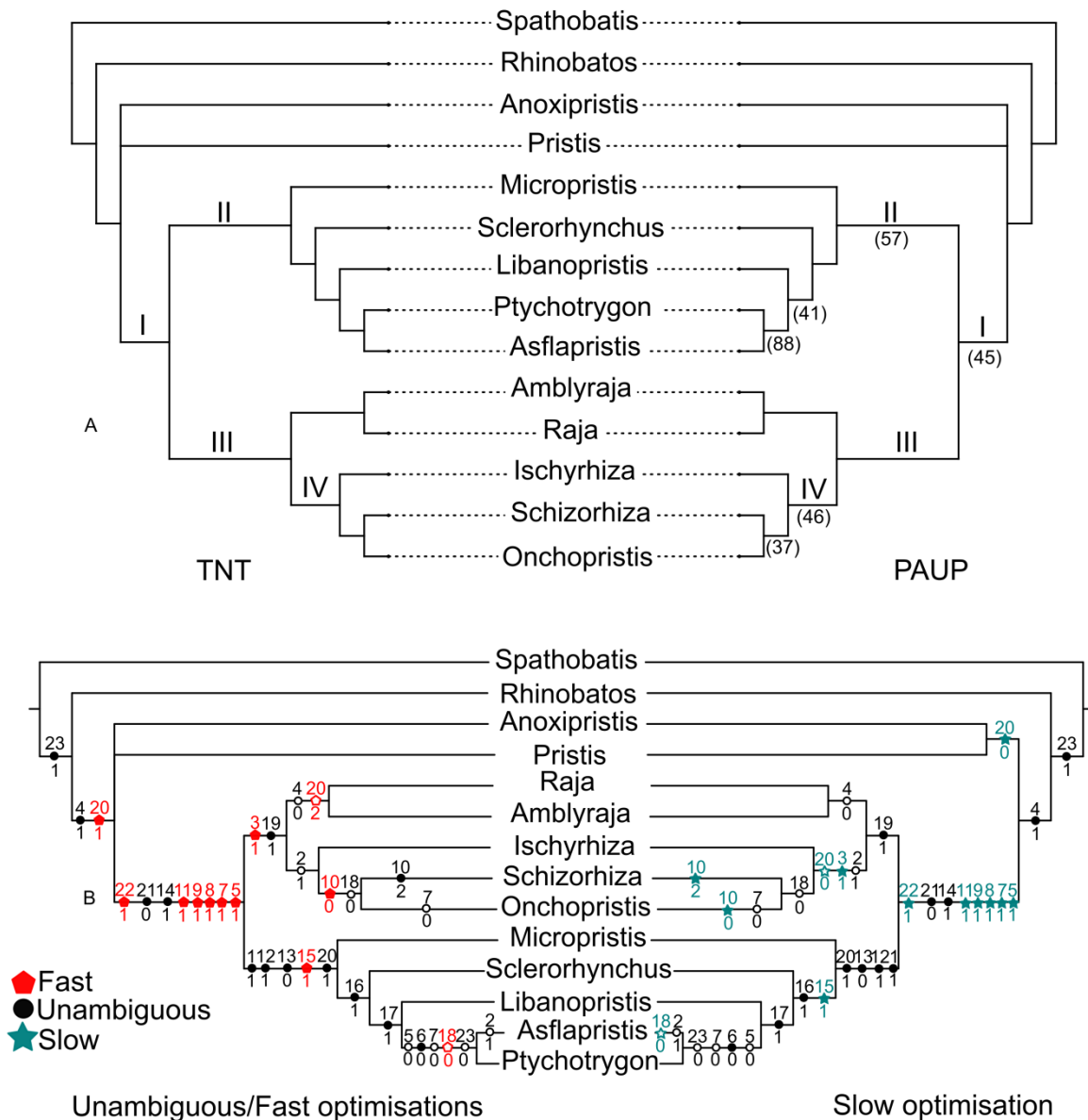


FIG. 10. A, TNT and PAUP most parsimonious tree (MPT). Roman numerals are the node numbers and below them in parenthesis are the Bootstrap values. B, character optimisations supporting the clades mapped in the TNT tree using WINCLADA.

TNT and PAUP phylogenetic analyses recovered a single most parsimonious tree with same topology of 33 steps and consistency (0.75) and retention indexes (0.84) (Fig. 10A). The

present analysis suggests that a phylogenetic structure can be recovered from current data for sclerorhynchoids. The topology recovered a large group that includes the sclerorhynchoids+Rajidae (Clade I, Bootstrap support (Bs)= 45) similar to Villalobos *et al.* (2019). Clade I, is supported by two unambiguous synapomorphies under the unambiguous optimisation (Uo): Char. 14, lack of articulation surface between the second hypobranchial and basibranchial and char. 21, lack of lateral uvula on teeth. Slow and fast optimisation add six extra synapomorphies: Char. 5, more than one series of denticles series associated to rostrum and cephalic series; Char. 7, presence of ventral rostral denticle series; Char. 8, presence of cephalic enlarge denticle series; Char. 9, presence of replacement of rostral cartilage denticle series; Char. 11, presence of pulp cavity in the enlarged rostral cartilages denticle series; Char. 22, lateral rostral denticles not embedded in alveoli of rostral cartilages (Fig. 10B). Two monophyletic groups are recovered within Clade I: *Amblyraja*, *Raja*, *Ischyrhiza*, *Onchopristis* and *Schizorhiza* (Clade III) and Clade II, that includes several members of Sclerorhynchidae (*sensu* Cappetta, 2012): *Micropristis*, *Sclerorhynchus*, *Libanopristis*, and Ptychotrygonidae (*Asflapristis* and *Ptychotrygon rostrispatula* sp. nov.) (Fig. 10A).

Clade II (Bs = 57) is supported by four characters (Uo): Char. 1, the presence of enlarge and paddle like proximal pectoral elements; Char. 12, the lack of direct articulation between the pectoral radials and the scapulocoracoid; Char. 13, reduced postorbital process; and Char. 20, leaf shaped rostrum that reaches its maximum width after the base (Fig. 10B). The fast optimisation adds an extra character: Char. 15, lack of articulation surface between the basibranchial and third hypobranchial. *Libanopristis* is recovered as sister group (Bs = 41) of Ptychotrygonidae and is supported by the presence of a transverse crest in the crown teeth labial face (Char 17). Ptychotrygonidae (Bs = 88) is supported by one unambiguous synapomorphy: the lack of enlarge lateral series of denticles in the rostral cartilages (Char. 6) (Fig. 10B). It is worth mentioning that Ptychotrygonidae is also differentiated by three other characteristics (Uo): presence of one series of enlarge denticles associated to rostral cartilages and cephalic region (Char. 5), the absence of ventral rostral denticles series in rostral cartilages (Char. 7) and the lack of a calcified suprascapula (Char. 23). The fast optimisation adds an extra character to this clade: Char. 18, absence of a lingual uvula. However, this character requires further review as is polymorphic within *Ptychotrygon* (e.g. *P. triangularis* present a cusp while *P. gueveli* and *P. rugosus* lacks it). Of the specimens reviewed only *Asflapristis cristadentis* constantly lacks medial cusp.

Clade III was not recovered by the Bootstrap analysis (<https://doi.org/10.5061/dryad.2t8c60f/2>), which instead recovered a polytomy between Rajidae and the eight sclerorhynchoid taxa included in the present analysis, and therefore no bootstrap value was assigned to it. Clade III includes the most peculiar fossils in the present study (*Onchopristis*, *Schizorhiza* and surprisingly *Ischyrhiza*) (Fig. 10A). This clade is supported by one unambiguous synapomorphy (Uo): Char. 19, the presence of enlarge denticles in the body. Under fast optimisation an additional synapomorphy was added: Char. 3, the presence of ‘wood-like’ cartilage in the rostrum. Clade IV (Bs = 46) includes *Onchopristis*, *Schizorhiza* and *Ischyrhiza* and is supported by one character (Uo): Char. 2, presence of ‘wood-like’ cartilage. Under slow optimisation an extra character and an unambiguous synapomorphy are added: Char. 3 presence of ‘wood-like’ cartilage in the rostrum; Char. 20, rostral cartilages with is widest point at the base (Fig. 10B). It is worth mentioning that the genera in group II present different types of rostral denticles replacement (Char. 10) which points towards a possible further differentiation within this clade.

DISCUSSION

Character discussion and mapping optimisation hypothesis

Character 1. Enlarged and paddle like proximal pectoral elements: (0) absent, (1) present. All know remains of pectoral fins of sclerorhynchoids present enlarged proximal pectoral elements (propterygium, mesopterygium and metapterygium), that present a narrow base and a wide distal end. There is a process that extends anteriorly in the propterygium and posteriorly in the metapterygium.

Optimisation

Unambiguous. This type of optimisation implies that slow and fast optimisations lead to the same number of steps. No pectoral remains are known for *Ischyrhiza*, *Onchopristis* and *Schizorhiza* or have been reported for *Anoxypristis* as such this character was coded as a (?) that under unambiguous optimisation creates ambiguity for these terminals. The current data suggesting that the enlargement and modification of proximal pectoral elements is a synapomorphy of group II (*Libanopristis*, *Sclerorhynchus*, *Micropristis* and Ptychotrygonidae) suggesting that this state appear later in the evolutionary history of the group. However, the present results do not disprove the possible presence of this state of character in *Ischyrhiza*, *Onchopristis* and *Schizorhiza*; further fossil discoveries are needed to corroborate or disprove the presence of this state in these taxa and other sclerorhynchoids.

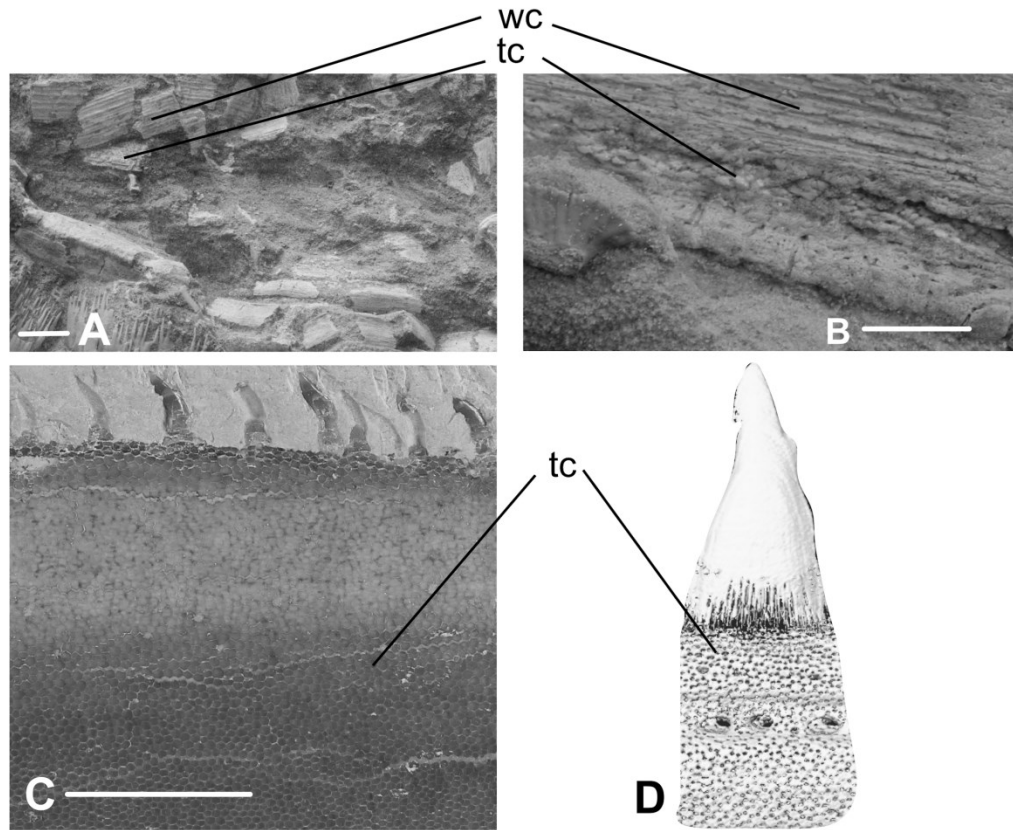


FIG. 11. Rostrum sections of: A, *Shizorhiza stromeri* NHMUK PV P 73625 (scale bar: 1cm). B, *Onchopristis numidus* NHMUK PV P 75502 (scale bar: 1cm). C, *Libanopristis hiram* NHMUK PV P 63610. (scale bar: 1cm) D, *Anoxypristis cuspidata*, A.442.6. Abbreviations: ld, Lateral denticle series; Pc, periphery cartilage; Rd, rostral denticle; Wc, Wood-like cartilage.

Character 2. ‘Wood like’ cartilage: (0) absent, (1) present.

Onchopristis, *Schizorhiza*, *Ischyrhiza* and *Asflapristis* present a peculiar type of cartilage on some regions of their chondroskeleton (Fig. 11 A-B). This resembles wood cortex with several vertical, parallel and well mineralized ridges. Underneath this layer are columns of tesserae (Fig. 11 C-D).

Optimisation

All three optimisations place the presence (2) of this type of cartilage as a homoplasy between Clade IV and *Asflapristis cristadentis*. We kept this character like this as it might suggests a tendency within sclerorhynchoids to develop this type of cartilage

Character 3. ‘Wood-like’ cartilage if present: (0) mouth, (1) rostrum.

This type of cartilage is not found in the same structures. *Onchopristis*, *Schizorhiza* and *Ischyrhiza* presented it in the rostral cartilages and *Asflapristis* in the mouth. Under current data, this character lacks phylogenetic information (uninformative), we opted to keep it as it arises from the use of reductive coding (Brazeau 2011), and because there are no other known skeletal remains to compare. The present analysis places the occurrence of this type of cartilage in the rostral cartilages (1) represents a synapomorphy for the *Onchopristis*, *Schizorhiza* and *Ischyrhiza* clade, and its presence in the mouth an autapomorphy for *Asflapristis* (0).

Optimisation

Unambiguous. The presence of ‘wood like’ cartilage in the rostral cartilages of *Onchopristis*, *Schizorhiza* and *Ischyrhiza* is placed as synapomorphy and its presence in the mouth cartilages as an autapomorphy of *Asflapristis*. However, it is not displayed in the tree as a result of the ambiguity in the other taxa. Current phylogenetic software deal with inapplicable characters (-) in the same way as they deal with unknown character (?) placing ambiguity in those terminals coded with (- or ?) as it assumes that all states of character are possible in them.

Slow. Its appearance later in the evolutionary history of the group places its presence in the rostral cartilages (1) as a synapomorphy of *Onchopristis*, *Schizorhiza* and *Ischyrhiza* with the plesiomorphic state being the presence in the mouth (0), this implies a subsequent independent loss on each terminal with the exception of *Asflapristis*.

Fast. Recovers a similar evolution of the character. However, the presence of ‘wood like’ cartilage in the rostral cartilages is gained earlier in the evolution of Clade I with its subsequent loss in *Raja* and *Amblyraja*.

Character 4. Enlarge denticle series associated to rostral cartilages and cephalic region: (0) absent, (1) present.

Several group of chondrichthyans have developed enlarged denticles series associated to the cephalic and rostral region. However, some sclerorhynchoids are the only known batoids that present more than one series.

Optimisation

All three optimisations recovered the presence of this denticle series as a synapomorphy between sclerorhynchoids and pristoids (1) with a subsequent loss in *Raja* and *Amblyraja* (0). However, the placement as a synapomorphy for these two groups is unlikely considering the vast amount of character differences between sclerorhynchoids and pristoids.

Character 5. Number of denticle series associated to rostral cartilages and cephalic region:
(0) one, (1) two or more.

The number of enlarged denticles series associated with the rostral region varies between the sclerorhynchoid. The Moroccan fossil remains of *Asflapristis cristadentis* and *Ptychotrygon rostrispatula* sp. nov. indicate that in Ptychotrygonidae only one series of enlarged denticles is present (0) the lateral cephalic. *Ptychotrygon rostrispatula* sp. nov. remains show no rostral or ventral denticles series attach to it. This suggests that the enlarged denticles recovered from mixed assemblages reported in the literature for the genus (Case 1978) correspond to the lateral anterior cephalic series. No cephalic remains of *Schizorhiza* are known, its rostral remains present only the rostral cartilages lateral denticles series (lack the denticle ventral series). Therefore, the number of enlarged denticles series associated with the rostral cartilages and lateral anterior cephalic region is unknown. *Sclerorhynchus* (Welten *et al.* 2015, Figs. 8-9; Underwood *et al.*, 2016 Fig. 1C), *Libanopristis* and *Onchopristis* have four enlarged rostral denticle series (1): one on the sides of the rostrum; other the anterior lateral parts of the cephalic region; and two on the ventral side (one in the centre and other on the sides). In *Micropristis* at least two series of enlarged denticles (1) have been observed (lateral rostral and lateral cephalic) this information is based in published records (no direct observation) (Cappetta 1980, plate 1, Figs. 1).

Optimisation

All three types of optimisation recovered the presence of more than one series as a synapomorphy of sclerorhynchoids and pristoids with a subsequent loss of several of these series in *Ptychotrygon* and *Asflapristis*. The presence of just one series of denticles should not be interpreted as shared characteristic between pristoids, *Asflapristis* and *Ptychotrygon* as they present different denticles series. Under current coding there is ambiguity for *Spathobatis*, *Rhinobatos*, *Raja* and *Amblyraja* as this character is coded as inapplicable (-) for these taxa (see character 3, for discussion on the implications of this).

Character 6. Rostral cartilages lateral denticles series: (0) absent, (1) present.

This character refers only to the lateral rostral series associated with the rostral cartilages. Its presence varies within sclerorhynchoids. No direct association between the rostral cartilages and this denticle series has been observed (0) for *Asflapristis* and *Ptychotrygon rostrispatula* sp. nov. In the remaining taxa of sclerorhynchoids either a direct association has been observed or reported in the literature (e.g. Cappetta 2012) (1).

Optimisation.

All three types of optimisation recovered the presence of the lateral rostral cartilages as shared characteristic of sclerorhynchoids and pristiods with a subsequent loss in *Ptychotrygon* and *Asflapristis*. There are other characters (e.g. Char 9 and 22) that suggest that instead of a synapomorphy the presence of this series is a homoplasy between sclerorhynchoids and pristiods. The absence of these series is recovered as a synapomorphy of *Asflapristis* and *Ptychotrygon*. Under current coding there is ambiguity for *Spathobatis*, *Rhinobatos*, *Raja* and *Amblyraja* as this character is coded as inapplicable (-) for these taxa (see character 3, for discussion on the implications of this).

Character 7. Ventral rostral denticles series: (0) absent, (1) present.

The presence of a ventral series of denticles has been reported for *Sclerorhynchus* (Welten *et al.* 2015, Figs. 8-9; Underwood *et al.* 2016 Fig. 1C), and a similar series has been observed in *Libanopristis* (1). From the literature review we could not determinate the state of character for *Micropristis* (?). The specimens reviewed of *Asflapristis*, *Ptychotrygon* and *Schizorhiza* (0) showed no evidence of this series. In *Onchopristis* there seems to be a uniform cover on the ventral surface of the rostrum some of which are enlarged (1) and are similarly shaped to those reported for *Ischyrhiza* (Sternes & Shimada 2018).

Optimisation

Unambiguous. The presence of this series is a shared characteristic between most of sclerorhynchoids. It also recovers ambiguity in *Micropristis* due to the lack of observations and in *Spathobatis*, *Rhinobatos*, *Raja* and *Amblyraja* as the character is coded as (-). In the case of *Spathobatis* and *Rhinobatos* the ambiguity extends in to the ancestors of pristiods which is followed by the absence of these series in sawfishes.

Fast and Slow. Considers this trait as a shared characteristic between several sclerorhynchoids with an independent loss in pristiods, *Asflapristis*, *Ptychotrygon* and *Schizorhiza*. Under current coding there is ambiguity for *Spathobatis*, *Rhinobatos*, *Raja* and *Amblyraja* as this character is coded as inapplicable (-) for these taxa (see character 3, for discussion on the implications of this).

Character 8. Enlarge cephalic denticle series: (0) absent (1) present.

This character refers to the presence the enlarge series on the lateral cephalic region. In *Ptychotrygon rostrispatula* sp. nov. remains show no rostral or ventral denticles series attach to it. This suggests that the enlarge denticles recovered from mixed assemblages reported in

the literature for the genus (Case 1978; plate 4, fig. 7a-c) correspond to the lateral anterior cephalic series. *Onchopristis* is a similar case no direct association has been reported. However, different morphologies of denticles for this genus have been reported some of which (e.g. Stromer 1927; plate 1, fig. 32a-b and Werner 1989; plate 20, fig. 9) are similar to the cephalic series reported for *Sclerorhynchus* by Welten *et al.* (2015).

Optimisation

Unambiguous. Under this optimisation the presence of this series is lost as a shared characteristic between most of sclerorhynchoids. It also recovers ambiguity in: *Micropristis*, *Ischyrhiza* and *Asflapristis* due to the lack of observations (?) and for *Spathobatis*, *Rhinobatos*, *Raja* and *Amblyraja* as the character is coded as (-). In the case of *Spathobatis* and *Rhinobatos* the ambiguity extends in to the ancestors of pristoids which is followed by the absence of this series in sawfishes.

Fast and slow. Considers the trait as a shared characteristic between several sclerorhynchoids. Under current coding there is ambiguity for *Spathobatis*, *Rhinobatos*, *Raja* and *Amblyraja* as this character is coded as inapplicable (-) for these taxa (see character 3, for discussion on the implications of this). The ambiguity in *Asflapristis*, *Ischyrhiza* and *Schizorhiza* is a result of the lack of observations to code this character (?).

Character 9. Replacement of rostral cartilage denticles series: (0) absent (1) present.

Rostral denticles in sclerorhynchoids are shed constantly, in contrast to those found in extant and fossil pristoids that are no replaced and grow continuously.

Optimisation

Unambiguous. Under this optimisation the presence of this series is lost as a synapomorphy for the sclerorhynchoid clade as there is ambiguity for the ancestral node between pristoids (0) and the sclerorhynchoids+rajoids clade as result of the ambiguity in the external group (*Spathobatis*, *Rhinobatos*).

Fast and slow. Considers the presence of this series as shared characteristic between several sclerorhynchoids with an independent loss in pristoids. Under current coding there is ambiguity for *Spathobatis*, *Rhinobatos*, *Raja*, *Amblyraja*, *Asflapristis* and *Ptychotrygon* as this character is coded as inapplicable (-) for these taxa (see character 3, for discussion on the implications of this).

Character 10. Type of replacement of rostral denticles: (0) type A, (1) type B, (2) type C.

This character is uninformative, we opted to keep it as the type replacement of rostral denticles variates among sclerorhynchoids taxa. In *Onchopristis* (NHMUK 75502; 75503) denticles of different sizes are constantly being added (2). It is unknown whether there is a temporality in the replacement or if denticles are just added as the space in the rostrum becomes available. In *Schizorhiza*, the denticles are arranged in batteries (0) one beneath the other (Smith *et al.* 2015). In *Sclerorhynchus* (Welten *et al.* 2015, text-figs. 8-9; Underwood *et al.*, 2015 text-fig. 1C), *Libanopristis*, *Micropristis* (pers. observations) and *Ischyrhiza* (Sternes & Shimada, 2018 text-fig. 2 A-D) rostral denticles are being replaced by denticles of the same size (1). It is worth to mention that *Shizorhiza* and *Ischyrhiza* are the only species in the present study that present rostral denticles with large roots with several lobes.

Optimisation.

All three types of optimisation recovered a similar evolutionary history for this character, in which the plesiomorphic character state is type B (denticles are replaced by denticles of the same size). The ambiguity in this character arises from the use inapplicability of this character for pristiods, *Spathobatis*, *Rhinobatos*, *Raja*, *Amblyraja*, *Asflapristis* and *Ptychotrygon*.

Slow. recovers less ambiguity as places the two different types of replacement observed in *Onchopristis* and *Shizorhiza* as an autapomorphy.

Fast. Places the battery replacement (0) as the plesiomorphic state for the *Onchopristis*+*Shizorhiza* clade.

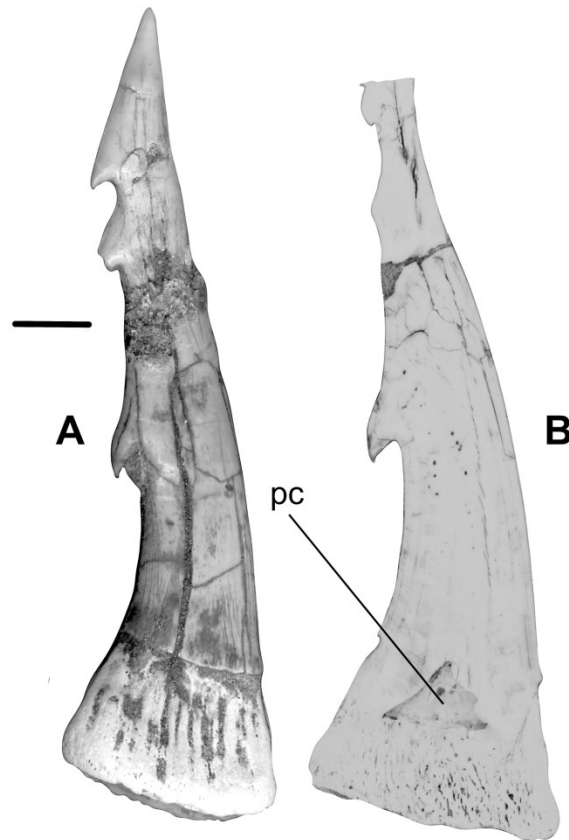


FIG. 12. *Onchopristis numidus*. A, lateral rostral denticle. B, section of lateral rostral denticle. Abbreviations: Pc, pulp cavity. (scale bar: 1 cm).

Character 11. Pulp cavities in the enlarged rostral cartilages denticles: (0) absent, (1) present. Several species of sclerorhynchoids (*Onchopristis* (Fig. 10); *Sclerorhynchus* and *Ischyrrhiza* (Slaughter & Steiner, 1968, Fig. 4 A-D; *Libanopristis*) present pulp cavities at base of the rostral denticles (1). While pristiods rostral denticles lack pulp cavity (0).

Optimisation

All three types of optimisation recovered a similar evolutionary history for this character, in which the presence of a pulp cavity (1) is a shared characteristic for sclerorhynchoids. The ambiguity in this character arises from the inapplicability of this character for *Spathobatis*, *Rhinobatos*, *Raja*, *Amblyraja*, *Asflapristis* and *Ptychotrygon*.

Unambiguous. Does not recover the presence as a synapomorphy. An adds ambiguity in to the outgroup (*Spathobatis* and *Rhinobatos*) and pristiods nodes due to the inapplicable (-) coding for them.

Slow and Fast. Recover less ambiguity as they place the presence of a pulp cavity as a synapomorphy for sclerorhynchoids. With the plesiomorphic state being the absence of cavity observed in pristiods.

Character 12. Mesopterygium-Metapterygium: (0) radials articulate between them, (1) no radials between them.

In all the known remains of sclerorhynchoids there is no evidence of direct articulation between the radials and the scapulocoracoid (1). Whether or not the lack of radials directly articulated to the scapulocoracoid is more widespread within the sclerorhynchoids is unknown as no pectoral remains of *Ischyrrhiza*, *Onchopristis* and *Schizorhiza* have been reported or for any of the species included in the present analysis (?).

Optimisation

All three types of optimisation recovered the same topology and distribution, in which the lack of direct articulation between the radials and the scapulocoracoid is recovered as a synapomorphy for group (II). However, the present results do not disprove the possible presence of this state of character in *Ischyrrhiza*, *Onchopristis* and *Schizorhiza*, further fossil discoveries are needed to corroborate or disprove whether state (1) is more widely distributed among sclerorhynchoids or an isolated feature of group (II).

Character 13. Postorbital process: (0) reduced, (1) well-developed.

The postorbital process is reduced in *Sclerorhynchus*, *Libanopristis*, *Micropristis*, *Asflapristis* and *Ptychotrygon* (0). *Spathobatis*, *Raja*, *Rhinobatos*, *Pristis* and *Anoxypristis* present a postorbital process (1). Although this character might be present in *Onchopristis*, *Schizorhiza* and *Ischyrrhiza* so far under current fossil evidence we cannot corroborate this (?).

Optimisation

All three types of optimisation recovered the same topology and distribution. The reduction of the postorbital process is recovered as a synapomorphy for group (II). However, the present results do not disprove the possible presence of this state of character in *Ischyrrhiza*, *Onchopristis* and *Schizorhiza*, further fossil discoveries are needed to corroborate or disprove whether state (1) is more widely distributed among sclerorhynchoids or an isolated feature of group (II).

Character 14. Second hypobranchial-basibranchial: (0) articulated, (1) fused.

The lack of articulation surface between the second hypobranchial and basibranchial (1) was observed in *Sclerorhynchus atavus* NHMUK PV P 49546 and *Ptychotrygon rostrispatula* sp. nov. its presence in both taxa could suggest that it could be widely distributed within

sclerorhynchoids and point of similarity between rajoids and sclerorhynchoids (Villalobos *et al.* 2019).

Optimisation

All three types of optimisation recovered a similar topology and distribution. The lack of articulation surface between the hypobranchial and basibranchial is recovered as a synapomorphy for the rajoid+sclerorhynchoid clade. The ambiguity within this clade arises from the current lack of fossil evidence to code this character in *Ischyrhiza*, *Onchopristis*, *Schizorhiza*, *Libanopristis*, *Micropristis*. The present results do not disprove the possible presence of this state for those, further fossil discoveries are needed to corroborate or disprove whether state (1) is more widely distributed among sclerorhynchoids. Both slow and fast optimisations recover the same character distribution.

Character 15. Third hypobranchial-basibranchial: (0) articulated, (1) fused.

In *Sclerorhynchus* and *Ptychotrygon rostrispatula* sp. nov. there is no articulation surface between the third hypobranchial and basibranchial (1). The outgroup presents an articulation surface between the third hypobranchial and basibranchial (0).

Optimisation

Unambiguous. Recovers the lack of articulation surface between the third hypobranchial and basibranchial (1) as a shared characteristic of *Sclerorhynchus*, *Libanopristis*, *Asflapristis* and *Ptychotrygon*. However, is not mapped due the ambiguity in *Micropristis* (?) see character 3 for discussion on ambiguity caused by this type of code.

Slow. Places the state (1) as a synapomorphy of the *Sclerorhynchus*, *Libanopristis*, *Asflapristis* and *Ptychotrygon* group.

Fast. Places the state (1) as a synapomorphy of the *Micropristis*, *Sclerorhynchus*, *Libanopristis*, *Asflapristis* and *Ptychotrygon* group.

Character 16. Ornament on teeth: (0) absent, (1) present.

Sclerorhynchoids generally present different ornamentations (ridges and crest) in their teeth specially in the labial face.

Optimisation

All three types of optimisation recovered a similar topology and distribution, in which the presence of present ridges and crests in the crown surface of the teeth is a synapomorphy for the clade that includes *Sclerorhynchus*, *Libanopristis*, *Asflapristis* and *Ptychotrygon* (1).

Character 17. Transverse crests: (0) absent, (1) present.

This character was proposed by Kriwet *et al.* (2009) as one of the synapomorphies of the family Ptychotrygonidae this transverse crest strongly differentiate the labial face from the lingual one (Fig. 12). *Libanopristis* also present this character (1) (Cappetta, 1980, pl. 2, fig. 5). However, in *Libanopristis* the crests are slightly more laterally directed, and its teeth are more symmetric than those of the Ptychotrygonidae. *Ptychotrygon* species in general present more than just one crest in the labial region.

Optimisation

All three optimisations recover the presence of a transverse crest on the labial surface (1) as a synapomorphy of *Libanopristis*, *Asflapristis* and *Ptychotrygon*.

Character 18. Lingual uvula: (0) absent, (1) present.

In *Asflapristis*, *Onchopristis* and *Schizorhiza* the lingual uvula is absent (0). In *Ptychotrygon* the development of the lingual uvula variates (0 & 1) (*Ptychotrygon gueveli* Cappetta, 2004 and *Ptychotrygon rugosa* Case *et al.*, 2001) (0).

Optimisation

All three optimisations implied two loss events of the lingual uvula (0), one in the *Onchopristis*+*Schizorhiza* clade and the last one in *Asflapristis*. We opted for this optimisation as both slow and fast fail to recover the uncertainty in *Ptychotrygon* as both states were present in this taxon.

Character 19. Enlarged denticles in body: absent (1), present (0).

In some rajoids some enlarge dermal denticles are present across the body (1). Cappetta noticed that the distribution of *Peyeria* Werner, 1989 and *Onchopristis* overlap and proposed the synonymy of *Peyeria* with *Onchopristis* (Cappetta 2012, text-fig. 371 B-D). The same commonality was found in the “Kem Kem Beds” supporting Cappetta’s (2012) hypothesis (Fig. 13). A similar occurrence has recently reported in the United States for the genus *Ischyrrhiza* (Sternes & Shimada 2018) (1). In no other sclerorhynchoid species this denticles have been reported (0). Considering the relatively good fossil record of some species in group (II) this character could indicate a very peculiar trait for *Onchopristis* and *Ischyrrhiza* (group I).

Optimisation

All three optimisations recover the presence of enlarge denticles in the body (1) as a synapomorphy of the *Raja*, *Amblyraja*, *Ischyrrhiza*, *Onchopristis* and *Schizorhiza* clade.

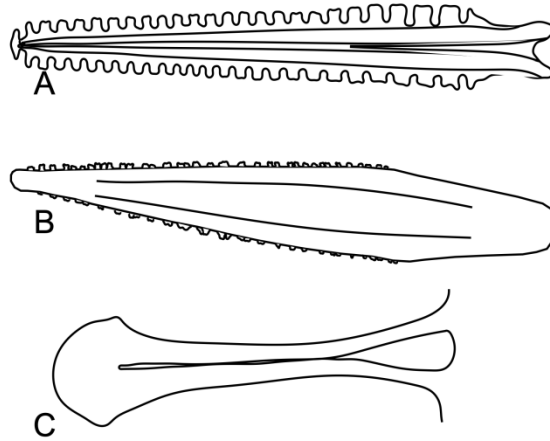


FIG. 13. Rostrum shape of: A, *Pristis* sp. *BRC-Pristis*, B. *Libanopristis hiram* NHMUK PV P 75075, C. *Rhinobatos glaucostigma* CNPE-IBUNAM 17810.

Character 20. Rostrum shape: (0) type A, (1) type B, and (2) type C (Fig. 13A-C).

Type A triangular reaching its maximum width at the base. Type B leaf shaped with its maximum width reached before the base of the rostrum. Type C Triangular-Concave (spatula shaped) with a precerebral fenestra extending.

The codification of this character is not ideal as is a composed character. The presence/absence of a precerebral fenestra has been used in previous works (Brito *et al.* 2013) and needs to be reevaluated as seems to be a convergence between groups with a rostral blade (sawfishes, sawsharks and sclerorhynchoids).

Libanopristis, *Micropristis*, *Sclerorhynchus* and *Ptychotrygon* (1) present a leaf shaped rostrum that reaches its maximum width beyond its base. *Onchopristis* and *Schizorhiza* (0) present a triangular rostrum similarly shaped to that of modern sawfishes and saw-sharks.

Optimisation

Unambiguous. Recovers the presence of a leaf shaped rostrum (1) as a synapomorphy of the Clade II. And places ambiguity regarding the transition between states (2) and (0).

Fast. Places the leaf shaped rostrum (1) as a synapomorphy for the pristids+Rajidae+sclerorhynchoids clade with a change to state (2) in Rajidae. Both unambiguous and fast optimisation fail to recover the Pristidae clade.

Slow. Recovers the least ambiguity. It suggests a different topology as a later evolution of the shape of the rostrum implies that the triangular shape of the rostrum evolved two times (1): one in the *Ischyrhiza*, *Onchopristis* and *Schizorhiza* and in the pristoids clades. This

optimisation also suggests that the triangular-Concave rostral cartilages with a precerebral fenestra, is the most common state among batoids and evolved once.

Character 21. Differentiated lateral uvulae on teeth: (0) absent, (1) present

This character was proposed by Claeson *et al.* (2013, char. 22) this character refers to the presence of lateral root directed projections of the crown commonly observed in several Rhinopristiformes (*sensu* Last *et al.* 2016).

Optimisation

All three optimisations recover the lack of latera uvula in the oral teeth (0) as a synapomorphy of the *rajoids+sclerorhynchoids* clade.

Character 22. Rostral denticles embedded in alveoli of rostral cartilage: (0) present, (1) absent.

Character proposed by Kriwet (2004), rostral denticles on the known sclerorhynchoids remains are superficially attached to the rostral cartilages, supported by connective tissue and dermis. In *Pristis* the denticles are deeply embedded into deep grooves on the margins of the rostral cartilages.

Optimisation

Unambiguous. recovers the ambiguity in the ancestral state between pristiods and sclerorhynchoids.

Fast and Slow. Recovered the same mapping for this character and place the superficial articulation of the lateral denticles series of the rostral cartilages (1) as a synapomorphy for the sclerorhynchoids and place the deeply embed lateral series of denticles in the rostral cartilages as the ancestral state (0) as the ancestral sate.

Character 23. Calcified suprascapula: (0) absent, (1) present (Based on AMC2012, char. 6).

This character is based on Aschliman's (2012) work, the character and states were changed as the present study involves fossil species and states such as fused medially and not fused medially can be difficult to be defined in fossil taxa. As we cannot prove that the absence or presence of a cartilage connecting the antimeres of the scapulocoracoid of Jurassic batoids and sclerorhynchoids. The lack of preservation of this cartilage in these groups could be caused by the absence of mineralization in the whole cartilage. Ontogenetic series of *Zapteryx brevirostris* shown a late calcification of this cartilage which could be the case for

Jurassic batoids and sclerorhynchoids in which this cartilage could be present but not calcified.

Libanoprists present a cartilage that resembles the suprascapula found in *Raja*. Due to the damage observed in the specimen it was not possible to determinate if this cartilage is in fact the suprascapula, because of this Claeson *et al.* (2013) coding was kept for this taxon.

Optimisation

All three optimisations differentiate the Jurassic batoids represented by *Spathobatis* from other ‘rhinobatoid-like’ batoids. The lack of a well mineralised suprascapula is occurred twice in the present analysis one in *Spathobatis* and Ptychotrygonidae. Whether this character is widely distributed within sclerorhynchoids remains unknown due to the lack of fossil evidence.

Phylogenetic relations

As previous analysis (Villalobos *et al.* 2019) the present results recovered a close relation between sclerorhynchoids and rajoids mostly due to similarities in their branchial skeleton (Char. 21). Whilst taxonomic and phylogenetic uncertainty will remain for other ‘sclerorhynchoid’ groups, the present analyses places *Ptychotrygon* as part of the Sclerorhynchoidei, based on its overall morphological traits (e.g. paddle-like pectoral elements and lack of articulation surface between basibranchial and the second and third hypobranchials). Whether if the rest of the members of Ptychotrygonidae (*Texatrygon* and *Ptychotrygonoides*) (*sensu* Cappetta 2012) can be placed in this suborder goes beyond the scope of the present study. The analyses suggest another taxonomic change in regard to the family Sclerorhynchidae, which could be divided in to two groups Clade IV and Clade II. However, this rearrangement could better frame in a more taxonomically focused work.

Each type of character coding implies pros and cons. Reductive coding, although in some cases leads to ambiguous optimisations of the characters, seems to provide logical hierarchical arrangement of characters (e.g. the presence-absence of structure is linked to whether or not changes occur in set structure), without making assumptions on the change order of characters (polarization). The fossilisation process by its nature implies the loss of character information, in which more derived character are often lost (Sansom *et al.* 2010; 2013). Because of this a character coding in which it is possible to reflect this hierarchical arrangement of characters might be desirable for phylogenetic analysis with fossil taxa. The

display and comparison of three types optimisations, revealed further information regarding the possible implications of character states changes and provide a richer discussion on the evolution of the group. However, special attention must be given to the type of optimisation if chosen, as fast and slow optimisation might make further assumptions regarding taxa with characters states coded as inapplicable and unknown.

CONCLUSION

Five specimens collected in the South and East of Asfla present teeth features (teeth small and oval-shaped, with a sharpened strong enamelled pyramidal crown and transverse crests on labial apron with a variably developed sagittal ridges. Apron is bent basally with a truncated projection, and lingual uvula short and broad with central interlocking depression) that place them in the genus *Ptychotrygon*. Representing the first reported skeletal remains for the genus. As with other fossils from the area the remains are three dimensional (Claeson *et al.* 2013; Villalobos *et al.* 2019).

These extremely well-preserved fossils revealed previously unobserved characters specially in the branchial skeleton, which were latter observed in *Sclerorhynchus atavus*. Regardless, the lack of enlarged rostral denticles series on the lateral edges of the rostral cartilages, the morphological feature observed in *Ptychotrygon rostrispatula* sp. nov. (e.g. paddle-like pectoral elements and lack of articulation surface between basibranchial and the second and third hypobranchials) place the species and genus as members of the sub order Sclerorhynchoidei (Cappetta, 1980).

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DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository:

<https://datadryad.org/review?doi=doi:10.5061/dryad.2t8c60f>

This published work and the nomenclatural act it contains, have been registered in:

ZooBank: <http://zoobank.org/References/XXXXXXXXXX>

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